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frontiers in Ecology and Evolution

EDITORIAL
published: 03 August 2016
doi: 10.3389/fevo.2016.00091

Editorial: Genetic Effects on Social Traits: Empirical Studies from Social Animals

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Keywords: ***Neofem*, Gal4/UAS system, social effect genes, tachykinin receptors, 5-methylcytosine**

The Editorial on the Research Topic

Genetic Effects on Social Traits: Empirical Studies from Social Animals

As genomic information becomes available for a growing number of social animals, so do opportunities to examine the genetic basis of social behavior. Nowhere is this more evident than in the field of social insect research that is actively bridging the once-separate sub-fields of socio- and molecular-biology (Linksvayer et al., 2012; Libbrecht et al., 2013; Kapheim et al., 2015; Rehan and Toth, 2015). In this Research Topic, we capture recent progress at this intersection of insect-based sociobiology and gene-level analyses. Fourteen contributing authors highlight how comparative, population, and epi-genetics approaches can be deployed to help resolve questions about the molecular evolution and gene-regulatory expression of social traits.

COMPARATIVE GENETICS

Korb builds on her discovery that termite "queen genes" are associated in their expression with female reproductive dominance. Not only are some of the *Neofem* genes from a species of drywood termite (*Cryptotermes secundus)* implicated in chemical communication and fertility, but their knock-down *in vivo* confirms that *Neofem2* and *Neofem4* are functionally involved in maintaining termite reproductive division of labor. *Neofem*-deficient queens seem unable to maintain their "royal" status, and show behavioral symptoms of ceding reproductive monopoly to other females within the colony. A comparison to other termite species reveals that this mechanism of gene-mediated control over reproduction is unlikely to be universal, because some *Neofem* genes are patchily distributed among different termite lineages. Other *Neofem* genes are, however, more widespread, and on-going gene manipulations in a range of social insect species will help determine whether the *Neofem* set evolved in whole or in part to regulate reproductive hierarchies and division of labor.

Camiletti and Thompson likewise show how comparisons among species, even non-social ones, can reveal which socially important genes are conserved from pre-social bauplans. Based on their discovery that honey bee royal substance can induce worker-like "sterility" in fruit flies, they promote *Drosophila melanogaster* as an unlikely but useful model for insect sociobiology. The incredible genetic tractability of *Drosophila* can be exploited in novel ways to screen for, and functionally manipulate the tissue-specific expression of, pheromone-responsive genes that regulate ovary de-activation and female sterility in social insects. Despite its phylogenetic position and pre-social biology, *Drosophila* can be used to test sociobiological predictions framed around gene function. Camiletti and Thompson's argument invokes the use of gene technologies

OPEN ACCESS

Edited and reviewed by:
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Specialty section:
This article was submitted to Social Evolution, a section of the journal Frontiers in Ecology and Evolution

Received: *24 June 2016*
Accepted: *18 July 2016*
Published: *03 August 2016*

Citation:
Thompson GJ and Richards MH (2016) Editorial: Genetic Effects on Social Traits: Empirical Studies from Social Animals. Front. Ecol. Evol. 4:91. doi: 10.3389/fevo.2016.00091

(e.g., GAL4-UAS targeted gene expression) that are well-established within the *Drosophila* research community but that are currently undeveloped for eusocial insects.

POPULATION GENETICS

Linksvayer and Wade note how the surge of large-scale -omics data sets in the field of insect sociobiology has for the most part been detached from social evolution theory. This disjunction offers new opportunities for integration, and they offer a population genetics model that may accelerate this integration. First, Linksvayer and Wade clarify how direct versus indirect selection is expected to affect the expression and evolution of protein-encoding genes. Second, they offer practical guidelines for how to partition RNA-sequenced genes into categories that best describe their social effect. For example, "queen genes" or "sterility genes" might best be described by their sib-social effects on queen fitness, and evolve at a rate that is distinct from genes with primarily maternal or offspring fitness effects. One prediction from this and related models is that indirectly selected loci should evolve more slowly (all else being equal) than loci under direct selection, simply because the selection coefficient is moderated by relatedness, which, for non-self interactions, will be less than $r = 1$.

Fouks and Lattorff put this prediction to the test by comparing rates of molecular evolution of three "social effect" genes between lineages of social and secondarily non-social (parasitic) bumble bees. Based on the roles that *vitellogenin*, *foraging*, and *salivary gland secretion 3* likely have in mediating divisions of labor within social species, Fouks and Lattorff predict a distinctly "social" syndrome based on the type and quantity of nucleotide substitutions that differs from a "solitary" syndrome that may characterize non-social lineages. From RNA-sequence information they show how patterns of sequence evolution vary as a function of social context, pleiotropy, sex-specific expression, and other genetic complexities. The contrasting substitution patterns of social and non-social *Bombus* suggest that their genes are indeed differentially responsive to social selection. Categorization of the genes as nominally social or non-social may however require even more subtle model-fitting to control for effects such as differences in effective population sizes of social and non-social species.

Howe et al. also adopt a locus-specific approach to understanding how genes might regulate selfless behavior within a social context. By analogy to gene-mediated aggression in *Drosophila*, Howe et al. predict that the neuropeptide *Tachykinin* and its receptor *Tachykinin-R99D* could mediate aggression in defensive castes. They test this idea by correlating gene expression with aggression in queen and different types of workers of the leaf-cutting ant *Acromyrmex echinatior*. Expression of *Tachykinin* and its receptor is correlated with aggression in workers but not queens, even when queens are physically manipulated into a behaviorally aggressive state. This suggests a caste-specific function for *Tachykinin*, and potentially for other genetic effects, highlighting again the role for indirect selection in social evolution.

EPIGENETICS

Li-Byarlay provides a timely review of the function of DNA methylation marks on division of labor, caste determination and aspects of learning and memory. She clarifies the epigenetic roles of 5-methylcytosine ($5^{M}C$) for specific genes in the initiation (*DNMT1*, *DNMT3*) and maintenance (*MET*) of methyl marks that dampen gene expression. These components of $5^{M}C$ are widely but variably distributed across the social taxa so far examined, suggesting that this mechanism plays an important but not universal role in social gene regulation. Importantly, Li-Byarlay smooths over previous disagreements by noting how technological platform and experimental design both contribute to estimates of $5^{M}C$ and re-iterates that social insects remain one of the best groups in which to study epigenetic control of gene regulation, behavior, development, and neurobiology.

CONCLUSIONS

Social evolution theory provides considerable scope for an eventual unification of classical theory and modern molecular genetic approaches to the evolutionary and mechanistic study of social life (Foster, 2011; Hofmann et al., 2014; Elgar, 2015). The six papers in this Research Topic certainly illustrate the field is heading in this direction, and that a future grand unification of sociobiological theory with empirical gene data is not only worthwhile, but feasible.

AUTHOR CONTRIBUTIONS

GT and MR came up with the topic idea, co-edited the Research Topic and co-wrote the cover editorial.

FUNDING

GT and MR are supported by Natural Sciences and Engineering Research Council (NSERC) of Canada Discovery Grants. We thank the Herbette Foundation (La Fondation Herbette) for facilitating GT's stay at the University of Lausanne.

REFERENCES

Elgar, M. A. (2015). Integrating insights across diverse taxa: challenges for understanding social evolution. *Front. Ecol. Evol.* 3:124. doi: 10.3389/fevo.2015.00124

Foster, K. R. (2011). The sociobiology of molecular systems. *Nat. Rev. Genet.* 12, 193–203. doi: 10.1038/nrg2903

Hofmann, H. A., Beery, A. K., Blumstein, D. T., Couzin, I. D., Earley, R. L., Hayes, L. D., et al. (2014). An evolutionary framework for studying mechanisms of social behavior. *Trends Ecol. Evol.* 29, 581–589. doi: 10.1016/j.tree.2014.07.008

Kapheim, K. M., Pan, H. L., Li, C., Salzberg, S. L., Puiu, D., Magoc, T., et al. (2015). Genomic signatures of evolutionary transitions from solitary to group living. *Science* 348, 1139–1143. doi: 10.1126/science.aaa4788

Libbrecht, R., Oxley, P. R., Kronauer, D. J. C., and Keller, L. (2013). Ant genomics sheds light on the molecular regulation of social organization. *Genome Biol.* 14:212. doi: 10.1186/gb-2013-14-7-212

Linksvayer, T. A., Fewell, J. H., Gadau, J., and Laubichler, M. D. (2012). Developmental evolution in social insects: regulatory networks from genes to societies. *J. Exp. Zool. B Mol. Dev. Evol.* 318B, 159–169. doi: 10.1002/jez.b.22001

Rehan, S. M., and Toth, A. L. (2015). Climbing the social ladder: the molecular evolution of sociality. *Trends Ecol. Evol.* 30, 426–433. doi: 10.1016/j.tree.2015.05.004

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